Using spor and prey counts to determine temporal and spatial variation in lion (Panthera leo) density

Bauer, Dominique ; Schiess-Meier, Monika ; Mills, David R ; Gusset, Markus

Abstract: In many African countries, large carnivores such as lions (Panthera leo (L., 1758)) are under serious threat through conflict with people, declining prey abundance, and exposure to disease. Spoor and prey count surveys were used to determine temporal and spatial variation in lion density in Khutse Game Reserve (KGR), Botswana, and the adjacent communal grazing area. Estimated lion density in KGR for the period September 2008 – June 2010 was 41% lower than for the period June 2007 – August 2008 (1.02 vs. 1.72 lions/100 km2). Prior to this population crash in mid-2008, estimated lion density in the communal grazing area (1.21 lions/100 km2) was 30% lower than inside KGR. The relative abundance of the three most abundant, preferred prey species of lions occurring in KGR decreased from 2001 to 2008 by 50%–79%. Based on two prey biomass estimates, the lion population in KGR was below the potential carrying capacity of the habitat after the crash in mid-2008. These results suggest that there could be a human-caused population sink around KGR, which might be strong enough to threaten the long-term survival of lions in the area; particularly if this edge effect is intensified by prey depletion and disease outbreaks, which might have caused the sudden decline in the lion population.

DOI: https://doi.org/10.1139/cjz-2013-0176

Originally published at:
Bauer, Dominique; Schiess-Meier, Monika; Mills, David R; Gusset, Markus (2014). Using spor and prey counts to determine temporal and spatial variation in lion (Panthera leo) density. Canadian Journal of Zoology, 92(2):97-104.
DOI: https://doi.org/10.1139/cjz-2013-0176

NRC Research Press

ARTICLE

Using spoor and prey counts to determine temporal and spatial variation in lion (*Panthera leo*) density

D. Bauer, M. Schiess-Meier, D.R. Mills, and M. Gusset

Abstract: In many African countries, large carnivores such as lions (*Panthera leo* (L., 1758)) are under serious threat through conflict with people, declining prey abundance, and exposure to disease. Spoor and prey count surveys were used to determine temporal and spatial variation in lion density in Khutse Game Reserve (KGR), Botswana, and the adjacent communal grazing area. Estimated lion density in KGR for the period September 2008 – June 2010 was 41% lower than for the period June 2007 – August 2008 (1.02 vs. 1.72 lions/100 km²). Prior to this population crash in mid-2008, estimated lion density in the communal grazing area (1.21 lions/100 km²) was 30% lower than inside KGR. The relative abundance of the three most abundant, preferred prey species of lions occurring in KGR decreased from 2001 to 2008 by 50%–79%. Based on two prey biomass estimates, the lion population in KGR was below the potential carrying capacity of the habitat after the crash in mid-2008. These results suggest that there could be a human-caused population sink around KGR, which might be strong enough to threaten the long-term survival of lions in the area; particularly if this edge effect is intensified by prey depletion and disease outbreaks, which might have caused the sudden decline in the lion population.

Key words: density, disease, edge effect, Kalahari, lion, *Panthera leo*, persecution, prey, spoor, track.

Résumé : Dans de nombreux pays africains, des grands carnivores comme les lions (*Panthera leo* (L., 1758)) sont fortement menacés en raison de conflits avec les humains, la diminution de l'abondance des proies et l'exposition aux maladies. Des levés des empreintes et de dénombrement des proies ont été utilisés pour déterminer les variations temporelles et spatiales de la densité des lions dans la Khutse Game Reserve (KGR), au Botswana, et la zone de pâturage communale qui la jouxte. La densité estimée de lions dans la KGR pour la période de septembre 2008 à juin 2010 était de 41 % plus faible que pour la période de juin 2007 à août 2008 (1,02 contre 1,72 lion/100 km²). Avant cet effondrement de la population au milieu de 2008, la densité estimée des lions dans la zone de pâturage communale (1,21 lion/100 km²) était de 30 % plus faible que dans la KGR. L'abondance relative des trois espèces les plus abondantes de proies prisées par les lions dans la KGR a diminué de 50 % – 79 % de 2001 à 2008. À la lumière de deux estimations de la biomasse de proies, la population de lions dans la KGR était inférieure à la capacité de charge potentielle de l'habitat après l'effondrement du milieu de 2008. Ces résultats donnent à penser qu'il pourrait y avoir un puits de population d'origine anthropique autour de la KGR dont l'effet pourrait être assez fort pour menacer la survie à long terme des lions dans la région, en particulier si cet effet de bordure est intensifié par la diminution des proies et les éclosions de maladies, qui pourraient avoir causé la diminution soudaine de la population de lions. [Traduit par la Rédaction]

Mots-clés : densité, maladie, effet de bordure, Kalahari, lion, *Panthera leo*, persécution, proie, empreinte, piste.

Introduction

Throughout Africa, large carnivores such as lions (*Panthera leo* (L., 1758)) are rapidly declining (Winterbach et al. 2013). From an estimated population of 200 000 African lions in 1975 (Myers 1975), less than 100 000 remained by the early 1990s (Nowell and Jackson 1996). Recent population estimates range from 38 000 (Chardonnet 2002) to 22 000 (Bauer and van der Merwe 2004). The most current estimates number the continent-wide lion population at 33 000 (IUCN/SSC Cat Specialist Group 2006) to 35 000 (Riggio et al. 2013).

One of the most important prerequisites for carnivore survival is prey availability. Although carnivore densities can vary over several orders of magnitude within species, they generally reflect the abundance of their prey in natural ecosystems (Fuller and Sievert 2001). It has been shown that the quality and quantity of prey resources available in an ecosystem determine carnivore density (Van Orsdol et al. 1985; Gros et al. 1996; Stander et al. 1997*a*; Karanth et al. 2004; Hayward et al. 2007). Across the whole order Carnivora, predator densities show a positive linear correlation with prey abundance, where 10 000 kg of prey support about 90 kg of a given carnivore species (Carbone and Gittleman 2002).

When wild prey numbers are reduced, lions among other carnivores turn to domestic livestock (Kissui 2008; Lagendijk and Gusset 2008; Gusset et al. 2009), particularly when protected areas are not safeguarded and farmlands are easily accessible. Livestock predation causes negative local attitudes toward lions and an increase in retaliatory and preventive killing by pastoralists (Gusset et al. 2008; Hemson et al. 2009; Maclennan et al. 2009).

Received 27 July 2013. Accepted 25 November 2013.

D. Bauer. Institute of Zoology, University of Hohenheim, 70599 Stuttgart, Germany; Leopard Ecology & Conservation, Khutse Game Reserve, Private Bag BR7, Gaborone, Botswana.
M. Schiess-Meier. Leopard Ecology & Conservation, Khutse Game Reserve, Private Bag BR7, Gaborone, Botswana; Institute of Evolutionary Biology and Environmental Studies, University of Zurich, 8057 Zurich, Switzerland.
D.R. Mills. Leopard Ecology & Conservation, Khutse Game Reserve, Private Bag BR7, Gaborone, Botswana.
M. Gusset. Leopard Ecology & Conservation, Khutse Game Reserve, Private Bag BR7, Gaborone, Botswana; Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Abingdon OX13 5QL, United Kingdom.
Corresponding author: M. Schiess-Meier (e-mail: monika.schiess@ieu.uzh.ch).

In recent years, Botswana's rapidly growing cattle industry has led to an increasing number of livestock losses due to predators on the communal farmland adjacent to Khutse Game Reserve (KGR), Botswana (Schiess-Meier et al. 2007). Although nominally protected inside reserves, the wide-ranging lions of the semiarid Kalahari (Ramsauer 2006; Funston 2011) are prone to human persecution when crossing the reserves' boundaries. We know of 52 lions that were killed on farmland in the vicinity of our study area on the southern border of KGR and Central Kalahari Game Reserve (CKGR) between 2005 and 2010, with 32 lions killed between May 2005 and October 2007 alone (lion hunting was banned from October 2000 to April 2005, with no records on number of lions killed in this area; the ban was reinstated in November 2007, thus only a fraction of lions killed were recorded). Reports from around CKGR suggest that this problem may exist on the periphery of the entire protected area (e.g., Muir 2010).

In August 2008, lion sightings in KGR became increasingly rare and several individuals were found dying with severe signs of malnutrition. We suspected that lion numbers were affected by a decline in prey abundance as observed elsewhere in Botswana (McNutt and Gusset 2012), but disease might have played a role as well (Ramsauer et al. 2007; Alexander et al. 2010). Considering the low lion density in the Kalahari (Ramsauer 2006; Funston 2011), the combined pressure of prey depletion, disease outbreaks, and human persecution might prove unsustainable and threaten the long-term viability of the KGR lion population.

The scientific focus of the present study was the hypothesis that variation in prey abundance and human persecution will lead to temporal and spatial variation in lion density. We used spoor counts to quantify the magnitude of the crash in the KGR lion population in mid-2008 and prey counts to quantify the magnitude of the suspected decline in prey abundance in KGR over time. Then, we used spoor counts to test the prediction that the lion density in the communal grazing area is lower than the density inside KGR. Finally, we tested the prediction that, as a consequence of the crash, the KGR lion population is below the potential carrying capacity of the habitat in terms of prey abundance.

Materials and methods

Study area

The study was conducted in Botswana's central Kalahari region, including KGR (central coordinates: 23°20′S, 24°25′E), the adjoining southern part of CKGR, and communal farmland bordering the two reserves to the southeast (for details see Schiess-Meier et al. 2007). In the protected area and communal farmland, the landscape is generally flat and lies about 1000 m above sea level. The vegetation is primarily *Acacia* Mill. savannah and Kalahari sandveld dotted with saltpans. The semiarid climate is characterized by a cold dry season (May–September) and a hot rainy season (October–April), with an annual rainfall of 321 ± 67 mm (Weilenmann et al. 2010).

Encompassing 2 600 km², KGR shares a common boundary with CKGR, forming the country's largest protected area complex with a total surface of more than 54 000 km² (Fig. 1). Whereas along KGR's western boundary human encroachment is relatively uncommon, there are numerous cattle posts (usually a small number of huts with associated livestock kraals) situated close to the southeastern border of the reserve. This is why the latter area was chosen for study. A number of factors have led to consistent livestock losses in recent years (Schiess-Meier et al. 2007): large home ranges of predators in this region (Ramsauer 2006; Weilenmann et al. 2010), close proximity of cattle posts to the still ungazetted buffer zone and reserve boundary, and overgrazing that has resulted in livestock entering the reserve. Wild prey numbers are low outside the reserve (Leopard Ecology & Conservation, unpublished data). In an attempt to reduce boundary transgression and livestock predation, 201 km of 2.4 m high electrified game fence was erected along the south and southeast borders of KGR and the southern part of CKGR in late 2009. This fence reduced wild prey numbers in the communal grazing area even further (Leopard Ecology & Conservation, unpublished data).

Spoor count survey

The general applicability of using spoor-based indices to estimate carnivore abundance (Stander 1998; Funston et al. 2001; Gusset and Burgener 2005; Balme et al. 2009; Houser et al. 2009) has been tested across a wide geographical scale and a large range of carnivore densities (Funston et al. 2010). To calculate lion densities from spoor densities (see below), Funston's general model for lions on sandy substrate was applied, explaining 97% of data variation across seven study sites: $t_i = 3.30x_i - 0.32$, where t_i is the spoor density and x_i is the estimated lion density at site *i* (Funston et al. 2010).

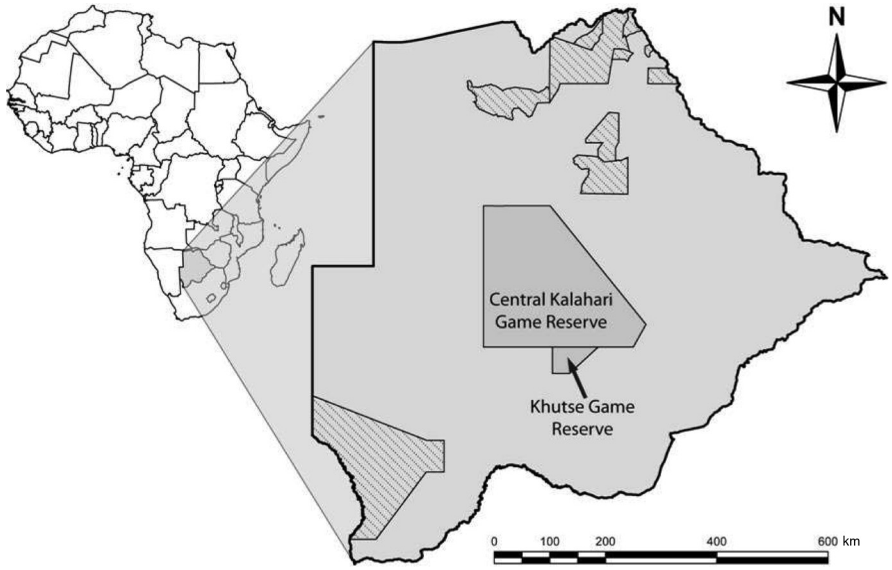
Spoor counts were conducted over a period of 3 years in two study sites (supplementary Table S1).[1] To quantify the magnitude of the crash in the KGR lion population in mid-2008, a first sampling period from June 2007 to August 2008 and a second sampling period from September 2008 to June 2010 were defined. As mentioned above, after August 2008, with known individuals dying or disappearing, lions became rare in KGR and around that time the spoor encounter rate dropped abruptly. During both sampling periods, eight transects (21.3 ± 1.9 km) with a total length of 170.7 km were covered repeatedly inside KGR (supplementary Fig. S1).[1] After the erection of the fence between KGR and the communal grazing area to the southeast in late 2009, a newly graded fire cutline between KGR and CKGR was incorporated into the transect network, increasing the total sampling distance to 193.0 km (24.1 ± 1.7 km). The second study site in the communal grazing area southeast of and adjacent to the reserve included six transects (19.1 ± 2.9 km) with a total length of 115.1 km that were covered repeatedly from June 2007 to May 2009 (supplementary Fig. S1).[1]

Spoor counts were conducted with the help of San trackers. The San are known for their outstanding tracking abilities and are highly accurate in identifying individuals and reconstructing complex behavior from spoor encounters (Stander et al. 1997*b*). All trackers participating in the study had several years of tracking experience and were thoroughly trained for this type of data collection. The trackers' ability was tested by following individual lions after locating their spoor when conducting spoor counts. Individuals were located with a success rate of 84.2% (n = 19) when tracking on sandy substrate and 60.0% (n = 5) when lions walked on the calcareous ground of the saltpans. The sex of the lions followed was always correctly determined. The spoor of adult individuals was successfully identified at a rate of 80.3%, based on spoor shape, size, and group composition.

Transects were sampled in the early morning hours to avoid disturbance by reserve visitors and because of the low angle of the sun. Spoor counts inside KGR were conducted on preexisting roads and fire cutlines, as their sandy substrate proved to be suitable for spoor detection and identification and as large carnivores frequently travel along roads. Although hard clay soil was predominant around the saltpans, it accounted for less than 5% of the road network. The bias due to changing spoor substrates is therefore likely to be minor. A four-wheel drive vehicle was driven at a mean speed of 15–20 km/h, with one tracker sitting on the bonnet and one on the roof scanning the road ahead. When spoor was encountered, species, sex, age, number of animals, location, and specific individuals were recorded. Individual spoor was counted

[1]Supplementary Table S1 and Fig. S1 are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2013-0176.

Fig. 1. Map of Botswana showing the Central Kalahari Game Reserve, Khutse Game Reserve, and other protected areas.



once a day and only spoor from the previous 24 h was recorded. Intersecting transects were sampled with a minimum lapse of 72 h. To avoid double-counting, the same transects were never sampled on consecutive days.

A radiotelemetry study on lion population dynamics in KGR revealed that the mean daily distance travelled by females was 8.2 ± 0.9 km (Ramsauer 2006). Because only spoor from the previous 24 h was recorded, choosing a study site by surrounding all transects with a buffer of 8.2 km would maximize the chance that the lions will still reside in the area at the time of sampling. Using the ArcView GIS software (version 9.3), two study sites of 2081 km² and 1394 km² for KGR and the communal grazing area, respectively, were demarcated accordingly (supplementary Fig. S1).[1]

Road penetration (rp) is expressed as the ratio between the distance covered and the size of the study area: rp = $A / \sum d_i$, where A is the size of the study site and d_i is the distance sampled on transect i (1 km surveyed : x km² survey area). It serves as an index of how intensively a specific site was covered when compared with other sampling areas. Spoor frequency and spoor density were calculated following Stander (1998). Spoor frequency is the number of kilometres per individual spoor (i.e., the distance one has to travel from one spoor encounter to the next). Spoor density is defined as the number of individual spoor per 100 km. Both indices were determined separately for each transect from which mean values and standard errors could be calculated.

The sampling intensity in both study sites was calculated in terms of a trade-off between effort and precision using bootstrap analysis (Sokal and Rohlf 1995). Measured by road penetration, it defines the distance that must be sampled in relation to the size of the study area. Sampling intensity was determined by randomly selecting two transects and increasing the sample progressively to 3, 4, …, x transects with replacement, simulating the spoor frequencies for 1000 replicates. After every increase the new road penetration, mean spoor frequencies, coefficients of variation, and 95% confidence intervals were calculated (Grieg-Smith 1957). The sample effort was set at the point where accuracy and precision of the estimates did not improve when the sample size was increased. Precision was defined at the point where the coefficient of variation (as the ratio between standard error and mean) reached an asymptote and dropped below 20% (Stander 1998).

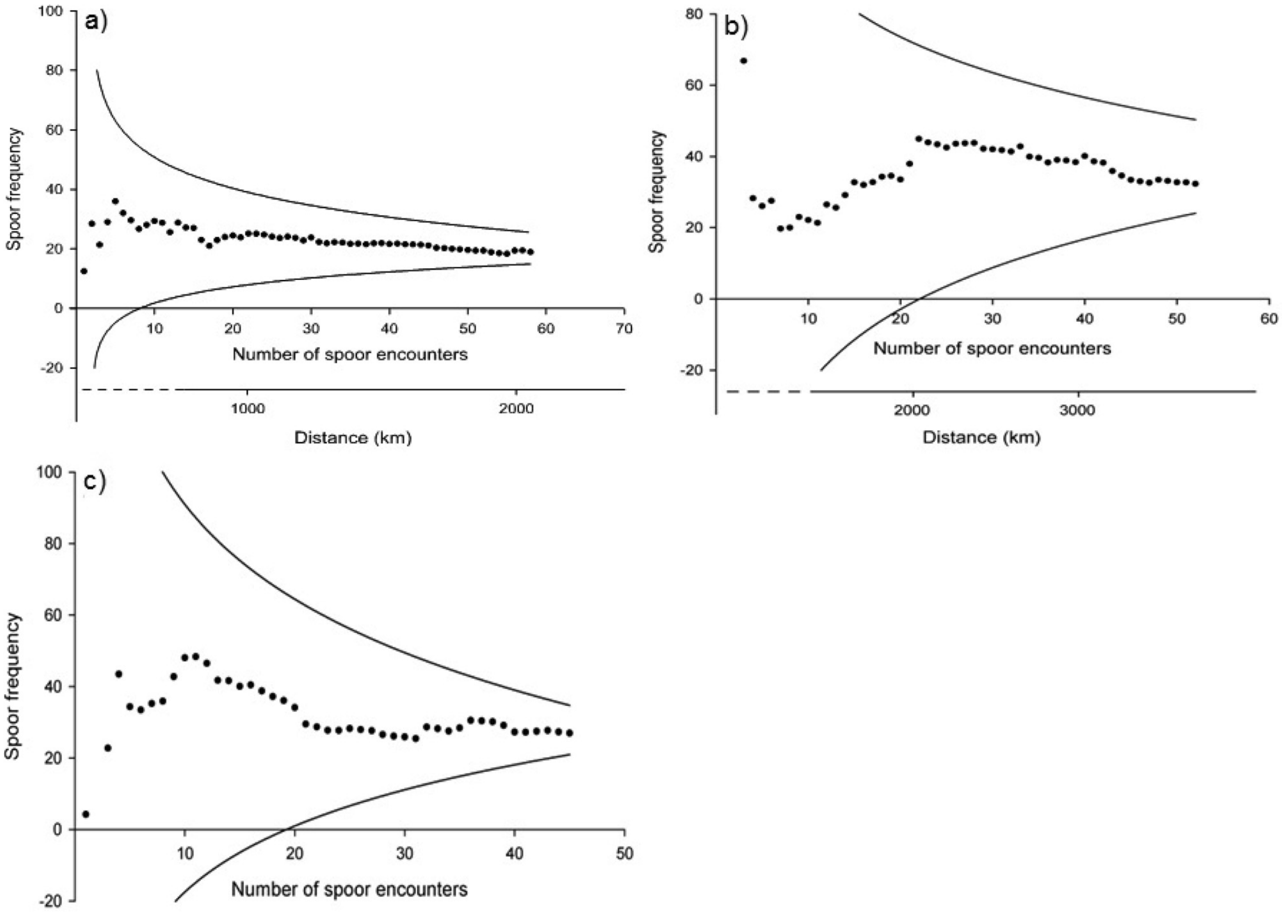
Means are given with standard error. Kolmogorov–Smirnov tests revealed that the data's residuals were not normally distributed, prompting the use of nonparametric statistics (Mann–Whitney U tests). All statistical tests were two-tailed, with the significance level set at $P < 0.05$, and were run in SYSTAT (version 12).

Prey count survey and carrying capacity

Prey counts were used to quantify the magnitude of the suspected decline in prey abundance in KGR over time. Prey abundance was estimated with the commonly used strip transect method, counting animals encountered within 200 m on either side of the transect. The same eight transects as described above were covered repeatedly inside KGR (supplementary Fig. S1)[1] during five sampling periods, each including both the cold dry and the hot rainy seasons: 2001 (8 months), 2002 (9 months), 2007–2008 (12 months), 2008–2009 (12 months), and 2009–2010 (7 months). Transects were sampled in the morning to avoid extreme temperatures that could bias animal distribution. A four-wheel drive vehicle was driven at a mean speed of 15–20 km/h with two observers on the roof. Monthly numbers per sampling period were calculated for the three most abundant (see below) prey species of lions in our study area, taken at least as frequently as expected based on their availability (Hayward and Kerley 2005): springbok (*Antidorcas marsupialis* (Zimmermann, 1780)), gemsbok (*Oryx gazella* (L., 1758)), and red hartebeest (*Alcelaphus buselaphus caama* Geoffroy Saint-Hilaire, 1803). Springbok and gemsbok, respectively, are the most commonly killed and preferred prey species of lions (Hayward and Kerley 2005); gemsbok are predominantly predated upon by lions in our study area. Prey counts were not conducted in the communal grazing area, as wild prey numbers are low outside the reserve and livestock is artificially maintained at high density (Leopard Ecology & Conservation, unpublished data).

Two different relationships between prey biomass derived from the 2009–2010 sampling period and lion density were used to predict the potential number of lions that KGR could support after the crash in mid-2008. (1) Hayward's regression equation $D = 10^{-2.158+0.377 \cdot \log x}$, where x is the biomass of the preferred prey species of lions (kg/km²) and D is the lion density per square kilometre (Hayward et al. 2007; M. Hayward, personal communication, 2010). Preferred prey species of lions (Hayward and Kerley 2005) occurring in KGR in notable numbers are gemsbok and giraffe (*Giraffa camelopardalis* (L., 1758)). (2) The relationship between carnivore density and prey biomass as defined by Carbone and Gittleman (2002), where one unit of prey biomass (10 000 kg/100 km²) supports a mean number of 3.4 lions/100 km². To account for the predominance of medium-sized to large prey (peak at

Fig. 2. The relationship between lion (*Panthera leo*) spoor frequency and sampling effort for the June 2007 – August 2008 sampling period inside Khutse Game Reserve (*a*), the September 2008 – June 2010 sampling period inside Khutse Game Reserve (*b*), and the communal grazing area adjacent to Khutse Game Reserve (*c*). The solid lines indicate 95% confidence intervals.



115 kg; Hayward and Kerley 2005), species below 100 kg adult female body mass were excluded from the biomass calculation. Masses of prey species were taken from Hayward et al. (2007) and prey densities were calculated using the DISTANCE software (version 5.0 beta 4).

Results

Spoor count survey

A total distance of 8135.3 km on 382 transects was sampled inside the KGR–CKGR complex and in the communal grazing area. Fresh lion spoor was recorded on 155 occasions and a total of 301 adult lion spoor were counted.

Mean spoor frequency did not show much variation with an increase in sampling intensity inside KGR. At minimum road penetration, spoor frequency had large confidence intervals; however, the confidence interval subsequently decreased with an increase in road penetration. At a ratio of 1 km : 13.9 km², mean spoor frequency was 22.4 ± 0.2. A further increase in road penetration altered the confidence interval by only 0.3%. The desired sampling intensity was therefore set at ≤1 km : 13.9 km² for KGR. For the spoor count survey in the communal grazing area, the desired sampling intensity was set at ≤1 km : 14.5 km².

Khutse Game Reserve

The effect of increased sampling effort on the spoor frequency was investigated by randomly selecting individual transects and increasing the sample size stepwise. In the first sampling period from June 2007 to August 2008, mean spoor frequency stabilized at 25 spoor samples, equivalent to 1180.0 km sampling distance (Fig. 2*a*). Precision increased considerably in the first 20 spoor samples and dropped below 20% at 25 spoor encounters (Fig. 3*a*). At 35 spoor samples (1495.9 km sampling distance), the coefficient of variation reached an asymptote, and although it continued to decrease, an increase in precision of only 5.5% was gained between 35 spoor encounters and the full sample (n = 58).

In the second sampling period from September 2008 to June 2010, mean spoor frequency stabilized only at 40 spoor samples, equivalent to 3143.2 km sampling distance (Fig. 2*b*), which stands in contrast to the first sampling period. Precision reached an asymptote at fewer spoor samples (n = 30) but after a greater sampling distance (2284.5 km) (Fig. 3*b*) than in the first sampling period. Hardly any spoor were encountered at the beginning of the second sampling period, and only sporadically thereafter.

Mean spoor frequency at maximum sampling distance showed a significant increase from one spoor per 18.9 ± 3.0 km in the first sampling period to one spoor per 33.0 ± 5.4 km in the second sampling period (U = 836.0, $n_{2007,2008}$ = 114, $n_{2008,2009,2010}$ = 118, $p < 0.0001$). Lions were estimated to occur at a mean density of 1.72 individuals/100 km² in the first sampling period. The estimate went down to 1.02 individuals/100 km² in the second sampling period (Table 1), corresponding to a reduction in lion density of 41%.

During the last 6 months of the second sampling period, when lions were encountered, pride structures and group compositions were estimated opportunistically through direct observation and

Fig. 3. The relationship between lion (*Panthera leo*) sampling precision and sample size for the June 2007 – August 2008 sampling period inside Khutse Game Reserve (*a*), the September 2008 – June 2010 sampling period inside Khutse Game Reserve (*b*), and the communal grazing area adjacent to Khutse Game Reserve (*c*). The broken horizontal lines represent a coefficient of variation of 20%.

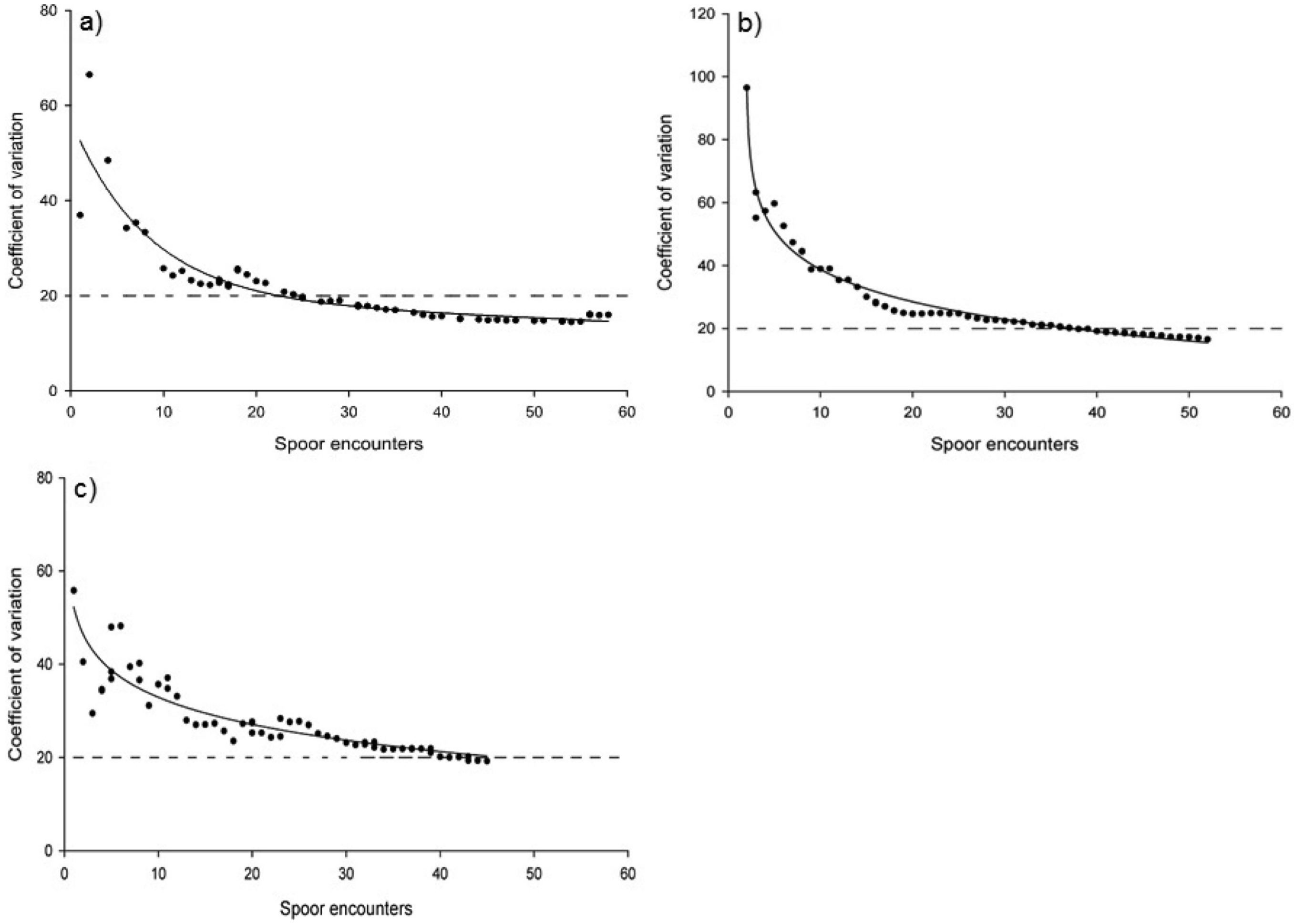


Table 1. Lion (*Panthera leo*) spoor density, estimated population density (number of individuals/100 km²), and estimated population size in the 2081 km² study area inside Khutse Game Reserve and the 1394 km² study area in the communal grazing area adjacent to Khutse Game Reserve.

	Density		Population size
	Spoor	Population	
Khutse Game Reserve			
June 2007–August 2008	5.36	1.72 (1.62–1.82)	36 (34–38)
September 2008–June 2010	3.05	1.02 (0.98–1.06)	21 (20–22)
Communal grazing area			
June 2007–May 2009	3.71	1.21 (1.00–1.43)	17 (14–20)

Note: Population density and size are reported with 95% confidence intervals.

individual recognition by whisker spots (Pennycuick and Rudnai 1970). A total of 19 lions (9 males and 10 females) in two prides, male coalitions, or as solitary individuals were known to use the study area inside KGR. This number corresponds well to the spoor-based estimate for the second sampling period (20–22 lions; Table 1).

Communal grazing area

Variation in spoor frequency for the communal grazing area remained relatively high even after considerably increasing the sample size (Fig. 2*c*). Precision reached an asymptote after 41 spoor encounters, equivalent to 1589.9 km sampling distance, and dropped below 20% after 44 spoor samples (1704.6 km sampling distance) (Fig. 3*c*). A gain in precision of only 4.5% between 41 spoor encounters and the full sample (n = 45) was achieved. For the 1394 km² study area in the communal grazing area, mean lion density was estimated at 1.21 individuals/100 km² (Table 1).

Mean spoor frequency in the communal grazing area did not show much variation over time. When compared with the results from the first sampling period inside KGR (one spoor per 18.9 ± 3.0 km; see above), mean spoor frequency in the communal grazing area (one spoor per 27.4 ± 5.2 km) showed a strong tendency to be higher at maximum sampling distance (U = 3268.5, n_{inside} = 114, n_{outside} = 69, p = 0.056), with a 30% lower lion density in the communal grazing area prior to the crash in mid-2008 (Table 1).

Prey count survey and carrying capacity

The relative abundance of the three most abundant, preferred prey species of lions decreased from 2001 to 2008 (Fig. 4). At the time of the crash in the lion population in mid-2008, springbok, gemsbok, and red hartebeest numbers had dropped by 60%, 79%, and 50%, respectively. The springbok and red hartebeest populations recovered in the 2009–2010 sampling period, while gemsbok numbers remained low.

For the 2009–2010 sampling period, during which a total distance of 2314 km on 100 transects was covered, nine mammal species above an adult female body mass of 8 kg and ostriches (*Struthio camelus* L., 1758) were recorded (Table 2). Estimated biomass

Fig. 4. The relative abundance per sampling period of the three most abundant, preferred prey species of lions (*Panthera leo*) occurring in Khutse Game Reserve (2001: 8 months; 2002: 9 months; 2007–2008: 12 months; 2008–2009: 12 months; 2009–2010: 7 months).

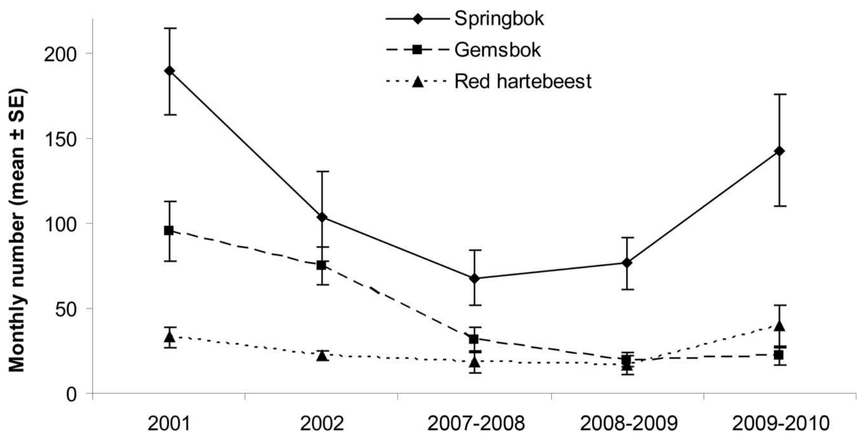


Table 2. Prey species recorded in the 2009–2010 sampling period, with number of encounters, number of individuals encountered, 75% adult female body mass (kg), estimated density (number of individuals/km²), and total estimated numbers in the 2081 km² study area inside Khutse Game Reserve.

	Number				
Species	Encounters	Individuals	Body mass	Density	Total
Gemsbok (*Oryx gazella*)	59	154	158	0.15 (0.10–0.22)	312 (208–458)
Red hartebeest (*Alcelaphus buselaphus caama*)	63	279	95	0.24 (0.14–0.40)	499 (291–832)
Ostrich (*Struthio camelus*)	53	103	70	0.10 (0.06–0.14)	208 (125–291)
Springbok (*Antidorcas marsupialis*)	103	999	26	1.05 (0.73–1.52)	2185 (1519–3163)
Steenbok (*Raphicerus campestris*)	201	233	8	0.43 (0.35–0.53)	895 (728–1103)
Common duiker (*Sylvicapra grimmia*)	10	12	16	0.01 (0.007–0.02)	21 (15–42)
Giraffe (*Giraffa camelopardalis*)	18	28	550	0.02 (0.006–0.04)	42 (12–83)
Greater kudu (*Tragelaphus strepsiceros*)	34	82	135	0.09 (0.05–0.14)	187 (104–291)

Note: Warthog (*Phacochoerus africanus*) and blue wildebeest (*Connochaetes taurinus*) were excluded due to small sample sizes (n = 2 and 3 encounters, respectively). Estimated density and total estimated numbers are reported with 95% confidence intervals.

of preferred prey species and all potential prey species was 34.8 kg/km² (95% CI = 19.0–56.7 kg/km²) and 69.7 kg/km² (95% CI = 39.0–113.6 kg/km²), respectively. Following Hayward et al. (2007), our study area inside KGR could support a potential lion density of 2.6 individuals/100 km² (95% CI = 2.1–3.2 individuals/100 km²), or a potential population of 55 (95% CI = 44–66). Using the relationship from Carbone and Gittleman (2002), potential lion density is 2.4 individuals/100 km² (95% CI = 1.3–3.9 individuals/100 km²), with a potential population of 49 (95% CI = 28–80). For comparison, the estimate from the spoor count survey between September 2008 and June 2010 numbered the lion population at 21 individuals (Table 1), suggesting that the lion population in KGR after the crash in mid-2008 was 57%–62% below the potential carrying capacity of the habitat.

Discussion

By means of a spoor-based survey, we estimated that between June 2007 and August 2008, a total of 34–38 lions occurred in our study area inside KGR. Lion density estimates for KGR (1.62–1.82 lions/100 km²) are relatively low compared with more mesic habitats (e.g., 7.0–9.9 lions/100 km² in the Serengeti National Park; Hanby et al. 1995); however, our estimates are comparable with those from other semiarid environments nearby, such as the Etosha National Park (1.8–2.1 lions/100 km²; Stander 1991; Trinkel 2013) or the tree savannah in the Kgalagadi Transfrontier Park (1.4–1.6 lions/100 km²; Funston et al. 2001; Ferreira et al. 2013). This gives us additional confidence in the results of our spoor-based survey (also see Ramsauer 2006; Funston 2011). Estimated lion density in our study area for the period October 2002 – February 2006 was 2.1 lions/100 km² (Ramsauer 2006; Ramsauer et al. 2007). Through repeated spoor counts, we were able to quantify the magnitude of the sudden decline in the KGR lion population in mid-2008. Population density estimates for the period September 2008 – June 2010 (0.98–1.06 lions/100 km²) were 41% lower than for the previous period, with only 20–22 lions remaining in our study area inside KGR after the crash. Our study demonstrates that repeated spoor counts can be useful to track changes in lion density over time and space, supporting the general applicability of using spoor-based indices to estimate carnivore abundance (Stander 1998; Funston et al. 2001, 2010; Gusset and Burgener 2005; Balme et al. 2009; Houser et al. 2009).

An estimated 14–20 lions occurred in the communal grazing area adjacent to KGR. Lion spoor frequency in this area did not show much variation over time and no sudden decline in mid-2008 was noted. This might be due to the fact that lions living close to the reserve boundaries and in the communal grazing area had access to a constant supply of prey in the form of livestock (Schiess-Meier et al. 2007), while the densities of wild prey inside the reserve declined. Or lions were otherwise attracted to the communal grazing area (e.g., Van der Meer et al. 2013), thus magnifying the decline inside the reserve and masking it outside. As predicted, mean spoor frequency in the communal grazing area showed a strong tendency to be higher at maximum sampling distance compared with the mean spoor frequency at maximum sampling distance inside KGR prior to the crash in mid-2008, with a 30% lower population density estimate in the communal grazing area (1.00–1.43 lions/100 km²). Lions learn to sporadically leave a reserve and hunt livestock in grazing areas along the reserve boundaries, and then to retreat to the relative safety of the protected area shortly after feeding (Loveridge et al. 2010). Considering the shared border of our two study sites, it is likely that most of the spoor recorded in the communal grazing area belonged to boundary transgressors that left the reserve when foraging (Schiess-Meier et al. 2007). The same individuals are known to roam both inside and outside the reserve (Weilenmann et al. 2010; Leopard Ecology & Conservation, unpublished data). Boundary transgression led to lions predating on livestock and, in turn, falling victim to retaliatory and preventive killing by pastoralists. This effect is exacerbated by males and females being killed indiscriminately (e.g., Kerth et al. 2013).

As suspected, the relative abundance of the three most abundant, preferred prey species of lions gradually decreased from 2001 to 2008 (by 50%–79%), with a low at the time of the crash in the lion population in mid-2008. This suggests that the crash might be related to prey depletion, with abruptly decreasing lion density over time (2.1, 1.72, and 1.02 lions/100 km² in 2002–2006, 2007–2008, and 2008–2010, respectively), possibly in conjunction with disease outbreaks (Ferreira and Funston 2010; Trinkel 2013). Likely because of reduced primary productivity and human activities, prey abundance in protected areas has declined elsewhere in Botswana (McNutt and Gusset 2012) and throughout Africa (Craigie et al. 2010). With little prey poaching inside the reserve, lower rainfall leading to reduced primary productivity probably caused the decline in prey abundance in our study area (Leopard Ecology & Conservation, unpublished data). As predicted and as a consequence of the crash, we found the KGR lion population to be below the potential carrying capacity of the habitat. This result should be viewed qualitatively, as predicting carnivore densities from prey abundance relies heavily on precise prey population estimates, calculations of prey biomass, and relationships between prey biomass and carnivore density (Karanth et al. 2004). Both approaches used in this study to calculate carrying capacity provided similar but relatively high lion density estimates, probably because some prey tend to accumulate on saltpans with good visibility, leading to relatively high prey population estimates. At the same time, our prey density estimates for the 2009–2010 sampling period were lower than those from other semiarid environments nearby (Funston et al. 2001; Trinkel 2010, 2013). Collectively, our findings suggest that prey density is high enough to allow for more lions; thus, a potential recovery of the KGR lion population is not hindered by prey abundance.

It remains to be seen in future surveys if the lion population in our study area will recover and lions will recolonize previously occupied habitat. Limiting factors to population recovery possibly are a lack of immigrating lions due to edge effects and disease outbreaks elsewhere in the KGR–CKGR complex; social perturbation and disease transmission due to the translocation of "problem" lions from outside the reserve; and continued human persecution of boundary transgressors despite the erection of the electrified fence—which cannot fully contain lions—in late 2009 (Woodroffe and Frank 2005; Balme et al. 2010; Weilenmann et al. 2010; Funston 2011; Packer et al. 2013). A spoor-based survey conducted throughout the KGR–CKGR complex in March 2012 provided an estimated density of 1.16 lions/100 km², numbering the total lion population at 634 (CKGR Research Group 2012). This estimate, while similar to our earlier estimate for the communal grazing area, is higher than the estimated lion density inside KGR after the crash in mid-2008. Continuing spoor counts, in combination with prey and disease surveys, will further elucidate the drivers of lion population dynamics in our study area and inform management if lions reach the potential carrying capacity of the habitat in terms of prey abundance. It will be important to determine if the fluctuations in lion density (e.g., due to prey depletion or disease outbreaks) are a naturally occurring phenomenon requiring little or no management intervention, or if this is a newly introduced problem that requires mitigating measures.

In conclusion, one concerning possibility is that there is a human-caused population sink around KGR (Woodroffe and Ginsberg 1998). As mentioned above, we know of 52 lions that were killed on farmland in the vicinity of our study area between 2005 and 2010. Our results suggest that as many lions were killed as were alive in the area during that time. This population sink might thus be strong enough to threaten the long-term survival of lions in the area; particularly if this edge effect is intensified by prey depletion and disease outbreaks. Therefore, even large protected areas might not be of sufficient size to protect populations of wide-ranging carnivores and boundaries need special safeguarding (Packer et al. 2013; Winterbach et al. 2013). Creating conservation buffer zones with nonlethal conflict mitigation strategies and managing human activities around protected area boundaries are essential.

Acknowledgements

We thank Botswana's Department of Wildlife and National Parks for permission to conduct the study and for continuing support. We are grateful to L. Boast, P. Funston, M. Hayward, K. Kesch, B. König, J. Kuppler, T. Pontynen, S. Ramsauer, J. Steidle, E. Tarszisz, and our trackers Mpheletsang, Phalatsa, Supula, Kebabaletswe, and Pogiso for assistance during various stages of the study. The study was funded by the Carl Herzog Foundation, the PSP Publishing Foundation, the Messerli Foundation, the African Cats and Conservation Foundation, and BGS Architekten. The manuscript benefitted from comments provided by C. Graf, J. Graf, S. Henley, and two anonymous reviewers.

References

Alexander, K.A., McNutt, J.W., Briggs, M.B., Standers, P.E., Funston, P., Hemson, G., Keet, D., and van Vuuren, M. 2010. Multi-host pathogens and carnivore management in southern Africa. Comp. Immunol. Microbiol. Infect. Dis. **33**: 249–265. doi:10.1016/j.cimid.2008.10.005. PMID:19038454.

Balme, G.A., Hunter, L.T.B., and Slotow, R. 2009. Evaluating methods for counting cryptic carnivores. J. Wildl. Manage. **73**: 433–441. doi:10.2193/2007-368.

Balme, G.A., Slotow, R., and Hunter, L.T.B. 2010. Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda–Mkhuze Complex, South Africa. Anim. Conserv. **13**: 315–323. doi:10.1111/j.1469-1795.2009.00342.x.

Bauer, H., and van der Merwe, S. 2004. Inventory of free-ranging lions (*Panthera leo*) in Africa. Oryx, **38**: 26–31. doi:10.1017/S0030605304000055.

Carbone, C., and Gittleman, J.L. 2002. A common rule for the scaling of carnivore density. Science, **295**: 2273–2276. doi:10.1126/science.1067994. PMID:11910114.

Chardonnet, P. 2002. Conservation of the African lion. International Foundation for the Conservation of Wildlife and Conservation Force, Paris.

CKGR Research Group. 2012. CKGR spoor survey March 2012. Report to the Department of Wildlife and National Parks, Gaborone, Botswana.

Craigie, I.D., Baillie, J.E.M., Balmford, A., Carbone, C., Collen, B., Green, R.E., and Hutton, J.M. 2010. Large mammal population declines in Africa's protected areas. Biol. Conserv. **143**: 2221–2228. doi:10.1016/j.biocon.2010.06.007.

Ferreira, S.M., and Funston, P.J. 2010. Estimating lion population variables: prey and disease effects in Kruger National Park, South Africa. Wildl. Res. **37**: 194–206. doi:10.1071/WR09030.

Ferreira, S.M., Govender, D., and Herbst, M. 2013. Conservation implications of Kalahari lion population dynamics. Afr. J. Ecol. **51**: 176–179. doi:10.1111/aje.12003.

Fuller, T.K., and Sievert, P.R. 2001. Carnivore demography and the consequences of changes in prey availability. *In* Carnivore conservation. *Edited by* J.L. Gittleman, S.M. Funk, D.W. Macdonald, and R.K. Wayne. Cambridge University Press, Cambridge. pp. 163–178.

Funston, P.J. 2011. Population characteristics of lions (*Panthera leo*) in the Kgalagadi Transfrontier Park. S. Afr. J. Wildl. Res. **41**: 1–10. doi:10.3957/056.041.0108.

Funston, P.J., Hermann, E., Babupi, P., Kruiper, A., Kruiper, H., Jaggers, H., Masule, K., and Kruiper, K. 2001. Spoor frequency estimates as a method of determining lion and other large mammal densities in the Kgalagadi Transfrontier Park. *In* Kalahari Transfrontier lion project. *Edited by* P.J. Funston. Endangered Wildlife Trust, Johannesburg. pp. 36–52.

Funston, P.J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D.W., Durant, S., Packer, C., Mosser, A., and Ferreira, S.M. 2010. Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. J. Zool. (Lond.), **281**: 56–65. doi:10.1111/j.1469-7998.2009.00682.x.

Grieg-Smith, P. 1957. Quantitative plant ecology. Butterworths, London.

Gros, P.M., Kelly, M.J., and Caro, T.M. 1996. Estimating carnivore densities for conservation purposes: indirect methods compared to baseline demographic data. Oikos, **77**: 197–206. doi:10.2307/3546058.

Gusset, M., and Burgener, N. 2005. Estimating larger carnivore numbers from track counts and measurements. Afr. J. Ecol. **43**: 320–324. doi:10.1111/j.1365-2028.2005.00581.x.

Gusset, M., Maddock, A.H., Gunther, G.J., Szykman, M., Slotow, R., Walters, M., and Somers, M.J. 2008. Conflicting human interests over the re-introduction of endangered wild dogs in South Africa. Biodivers. Conserv. **17**: 83–101. doi:10.1007/s10531-007-9232-0.

Gusset, M., Swarner, M.J., Mponwane, L., Keletile, K., and McNutt, J.W. 2009. Human–wildlife conflict in northern Botswana: livestock predation by endangered African wild dog *Lycaon pictus* and other carnivores. Oryx, **43**: 67–72.

Hanby, J.P., Bygott, J.D., and Packer, C. 1995. Ecology, demography, and behavior of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti plains. *In* Serengeti II: dynamics, management, and conservation of an ecosystem. *Edited by* A.R.E Sinclair and P. Arcese. University of Chicago Press, Chicago. pp. 315–331.

Hayward, M.W., and Kerley, G.I.H. 2005. Prey preferences of the lion (*Panthera leo*). J. Zool. (Lond.), **267**: 309–322. doi:10.1017/S0952836905007508.

Hayward, M.W., O'Brien, J., and Kerley, G.I.H. 2007. Carrying capacity of large African predators: predictions and tests. Biol. Conserv. **139**: 219–229. doi:10.1016/j.biocon.2007.06.018.

Hemson, G., Maclennnan, S., Mills, G., Johnson, P., and Macdonald, D.W. 2009. Community, lions, livestock and money: a spatial and social analysis of attitudes to wildlife and the conservation value of tourism in a human–carnivore conflict in Botswana. Biol. Conserv. **142**: 2718–2725. doi:10.1016/j.biocon.2009.06.024.

Houser, A.M., Somers, M.J., and Boast, L.K. 2009. Spoor density as a measure of true density of a known population of free-ranging wild cheetah in Botswana. J. Zool. (Lond.), **278**: 108–115. doi:10.1111/j.1469-7998.2009.00554.x.

IUCN/SSC Cat Specialist Group. 2006. Conservation strategy for the lion in eastern and southern Africa. International Union for Conservation of Nature (IUCN), Pretoria.

Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A., and Hines, J.E. 2004. Tigers and their prey: predicting carnivore densities from prey abundance. Proc. Natl. Acad. Sci. U.S.A. **101**: 4854–4858. doi:10.1073/pnas.0306210101. PMID:15041746.

Kerth, G., Gusset, M., Garbely, J., König, B., Gabanapelo, T., and Schiess-Meier, M. 2013. Genetic sexing of stock-raiding leopards: not only males to blame. Conserv. Genet. Resour. **5**: 1101–1105. doi:10.1007/s12686-013-9979-4.

Kissui, B.M. 2008. Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. Anim. Conserv. **11**: 422–432.

Lagendijk, G.G.D., and Gusset, M. 2008. Human–carnivore coexistence on communal land bordering the Greater Kruger Area, South Africa. Environ. Manage. **42**: 971–976. doi:10.1007/s00267-008-9204-5. PMID:18810524.

Loveridge, A.J., Hemson, G., Davidson, Z., and Macdonald, D.W. 2010. African lions on the edge: reserve boundaries as "attractive sinks". *In* Biology and conservation of wild felids. *Edited by* D.W. Macdonald and A.J. Loveridge. Oxford University Press, Oxford. pp. 283–304.

Maclennan, S.D., Groom, R.J., Macdonald, D.W., and Frank, L. 2009. Evaluation of a compensation scheme to bring about pastoralist tolerance of lions. Biol. Conserv. **142**: 2419–2427. doi:10.1016/j.biocon.2008.12.003.

McNutt, J.W., and Gusset, M. 2012. Declining body size in an endangered large mammal. Biol. J. Linn. Soc. **105**: 8–12. doi:10.1111/j.1095-8312.2011.01785.x.

Muir, M.J. 2010. Human–predator conflict and livestock depredations: methodological challenges for wildlife research and policy in Botswana. J. Int. Wildl. Law Pol. **13**: 293–310. doi:10.1080/13880292.2010.524573.

Myers, N. 1975. The silent savannas. Int. Wildl. **5**: 5–10.

Nowell, K., and Jackson, P. 1996. Wild cats: status survey and conservation action plan. International Union for Conservation of Nature (IUCN), Gland, Switzerland.

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S.T., et al. 2013. Conserving large carnivores: dollars and fence. Ecol. Lett. **16**: 635–641. doi:10.1111/ele.12091. PMID:23461543.

Pennycuick, C.J., and Rudnai, J. 1970. A method of identifying individual lions (*Panthera leo*) with an analysis of the reliability of identification. J. Zool. (Lond.), **160**: 497–508. doi:10.1111/j.1469-7998.1970.tb03093.x.

Ramsauer, S. 2006. Living at low density: a study of within and between pride dynamics in Kalahari lions. Ph.D. thesis, University of Zurich, Zurich, Switzerland.

Ramsauer, S., Bay, G., Meli, M., Hofmann-Lehmann, R., and Lutz, H. 2007. Seroprevalence of selected infectious agents in a free-ranging, low-density lion population in the Central Kalahari Game Reserves in Botswana. Clin. Vaccine Immunol. **14**: 808–810. doi:10.1128/CVI.00307-06. PMID:17460117.

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., de Iongh, H., Lichtenfeld, L., and Pimm, S. 2013. The size of savannah Africa: a lion's (*Panthera leo*) view. Biodivers. Conserv. **22**: 17–35. doi:10.1007/s10531-012-0381-4.

Schiess-Meier, M., Ramsauer, S., Gabanapelo, T., and König, B. 2007. Livestock predation–insights from problem animal control registers in Botswana. J. Wildl. Manage. **71**: 1267–1274. doi:10.2193/2006-177.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry. 3rd ed. Freeman, New York.

Stander, P.E. 1991. Demography of lions in the Etosha National Park, Namibia. Madoqua, **18**: 1–9.

Stander, P.E. 1998. Spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. J. Appl. Ecol. **35**: 378–385. doi:10.1046/j.1365-2664.1998.00313.x.

Stander, P.E., Haden, P.J., Kaqece, //., and Ghau, //. 1997*a*. The ecology of asociality in Namibian leopards. J. Zool. (Lond.), **242**: 343–364. doi:10.1111/j.1469-7998.1997.tb05806.x.

Stander, P.E., Ghau, //., Tsisaba, D., ≠oma, //., and |ui, |. 1997*b*. Tracking and the interpretation of spoor: a scientifically sound method in ecology. J. Zool. (Lond.), **242**: 329–341. doi:10.1111/j.1469-7998.1997.tb05805.x.

Trinkel, M. 2010. Prey selection and prey preferences of spotted hyenas *Crocuta crocuta* in the Etosha National Park, Namibia. Ecol. Res. **25**: 413–417. doi:10.1007/s11284-009-0669-3.

Trinkel, M. 2013. Climate variability, human wildlife conflict and population dynamics of lions *Panthera leo*. Naturwissenschaften, **100**: 345–353. doi:10.1007/s00114-013-1034-5. PMID:23503752.

Van der Meer, E., Fritz, H., Blinston, P., and Rasmussen, G.S.A. 2013. Ecological trap in the buffer zone of a protected area: effects of indirect anthropogenic mortality on the African wild dog *Lycaon pictus*. Oryx. In press. doi:10.1017/S0030605312001366.

Van Orsdol, K.G., Hanby, J.P., and Bygott, J.D. 1985. Ecological correlates of lion social organisation (*Panthera leo*). J. Zool. (Lond.), **206**: 97–112. doi:10.1111/j.1469-7998.1985.tb05639.x.

Weilenmann, M., Gusset, M., Mills, D.R., Gabanapelo, T., and Schiess-Meier, M. 2010. Is translocation of stock-raiding leopards into a protected area with resident conspecifics an effective management tool? Wildl. Res. **37**: 702–707. doi:10.1071/WR10013.

Winterbach, H.E.K., Winterbach, C.W., Somers, M.J., and Hayward, M.W. 2013. Key factors and related principles in the conservation of large African carnivores. Mammal Rev. **43**: 89–110. doi:10.1111/j.1365-2907.2011.00209.x.

Woodroffe, R., and Frank, L.G. 2005. Lethal control of African lions (*Panthera leo*): local and regional population impacts. Anim. Conserv. **8**: 91–98. doi:10.1017/S1367943004001829.

Woodroffe, R., and Ginsberg, J.R. 1998. Edge effects and the extinction of populations inside protected areas. Science, **280**: 2126–2128. doi:10.1126/science.280.5372.2126. PMID:9641920.